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Article Sub-Title		
Article CopyRight	Springer-Verlag (This will be the copyright line in the final PDF)	
Journal Name	Oecologia	
Corresponding Author	Family Name	**Vicente**
	Particle	
	Given Name	**J.**
	Suffix	
	Division	
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Schedule	Received	17 November 2009
	Revised	
	Accepted	7 May 2010

Abstract	The influence of short- and long-term (cohort) effects of climate and density on the life-histories of ungulates in temperate regions may vary with latitude, habitat, and management practices, but the life-histories of ungulates in the Mediterranean region are less well known. This study examined the short- and long-term effects of rainfall and absolute density on hinds in two of the southernmost populations of red deer (*Cervus elaphus hispanicus*) in Europe. One population received supplementary forage. Unlike more northerly latitudes, where red deer hinds lose body mass in winter as a result of adverse weather, in the Spanish populations, hinds did not lose body mass. Hinds in the population that received supplementary forage were heavier and more likely to become pregnant than were the hinds in the unsupplemented population. The likelihood of pregnancy occurring was strongly influenced by hind body mass; the proportion of yearlings that became pregnant was consequently lower in the unsupplemented population than in the population that received supplementary forage. Cohort effects on hind body mass (negative for density and positive for rainfall at birth) and on the probability of pregnancy (negative for density at birth) were apparent only in the unsupplemented population, which implies that supplemental feeding may partially compensate for negative density-dependent factors during early growth, and that supplemented deer hinds may experience reduced selection pressures. These results reflect the particular seasonal variation in the abundance and quality of food in Mediterranean habitats. The delayed effects of climate and density at birth on adult hind body mass and the prevalence of pregnancy probably affects population dynamics and constitutes a mechanism by which cohort effects affect the population dynamics in Iberian red deer. The management of Iberian red deer populations should incorporate cohort effects and supplemental feeding practices, which can buffer density- and climate-dependent effects and reduce natural selection pressures.

Keywords (separated by '-')	Climate - Cohort effects - Density - Management - Supplemental feeding
Footnote Information	Communicated by Jean-Michel Gaillard.

Oecologia
DOI 10.1007/s00442-010-1663-8

POPULATION ECOLOGY - ORIGINAL PAPER

Effects of density, climate, and supplementary forage on body mass and pregnancy rates of female red deer in Spain

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Received: 17 November 2009 / Accepted: 7 May 2010

Abstract The influence of short- and long-term (cohort) effects of climate and density on the life-histories of ungulates in temperate regions may vary with latitude, habitat, and management practices, but the life-histories of ungulates in the Mediterranean region are less well known. This study examined the short- and long-term effects of rainfall and absolute density on hinds in two of the southernmost populations of red deer (*Cervus elaphus hispanicus*) in Europe. One population received supplementary forage. Unlike more northerly latitudes, where red deer hinds lose body mass in winter as a result of adverse weather, in the Spanish populations, hinds did not lose body mass. Hinds in the population that received supplementary forage were heavier and more likely to become pregnant than were the hinds in the unsupplemented population. The likelihood of pregnancy occurring was strongly influenced by hind body mass; the proportion of yearlings that became pregnant was consequently lower in the unsupplemented population than in the population that received supplementary forage. Cohort effects on hind body mass (negative for density and positive for rainfall at birth) and on the probability of pregnancy (negative for density at birth) were apparent only in the unsupplemented population, which implies that supplemental feeding may partially compensate for negative density-dependent factors during early growth, and that supplemented deer hinds may experience reduced selection pressures. These results reflect the particular seasonal variation in the abundance and quality of food in Mediterranean habitats. The delayed effects of climate and density at birth on adult hind body mass and the prevalence of pregnancy probably affects population dynamics and constitutes a mechanism by which cohort effects affect the population dynamics in Iberian red deer. The management of Iberian red deer populations should incorporate cohort effects and supplemental feeding practices, which can buffer density- and climate-dependent effects and reduce natural selection pressures.

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Introduction

Climatic conditions and population density affect the life-history traits and population dynamics of wild ungulates (e.g. Saether 1997; Gaillard et al. 2000b) and interactions between the environment and density-dependence may occur (e.g. Coulson et al. 2005; Boyce et al. 2006). The

Journal : Large 442 | Dispatch : 18-5-2010 | Pages : 10
Article No. : 1663 | ☐ LE | ☐ TYPESET
MS Code : OEC-HY-2009-1135 | ☑ CP | ☑ DISK

effects of seasonal variations in climate on ungulate life-history traits in temperate regions may vary between latitudes and habitats (e.g. Mysterud et al. 2001; Loe et al. 2006). Most research has focused on populations in north temperate regions, where ungulates can face periods of nutritional constraint in winter as a result of snow cover and reduced accessibility to food (e.g. Solberg and Saether 1994; Schmidt and Hoi 2002), but conditions in summer can greatly influence life-history traits (e. g. Solberg et al. 1999; Schmidt et al. 2001). Much less attention has been paid to large herbivores in Mediterranean regions (Martinez-Jauregui et al. 2009), where the availability of food may be influenced by climate in different ways, with substantial inter-annual variation, and the summer period being the hardest owing to limited precipitation and reduced quality of food (Bugalho and Milne 2003). Population density can affect ungulate life-history traits such as body mass, survival, and reproduction (see Bonenfant et al. 2009 for a recent review). High relative densities (number of individuals per unit of food; Herfindal et al. 2006) can exacerbate the impact of environmental effects (Coulson et al. 2001), particularly during periods of low food availability.

Environmental conditions during early development can significantly affect growth and survival, and phenotypic quality (e.g. body size) and, consequently, the reproductive performance of individuals later in life (e.g. Albon et al. 1987; Loison et al. 1999). Among ungulates, weather conditions at birth can influence body mass (e.g. Pettorelli et al. 2002; Solberg et al. 2004) and reproductive success (e.g. Albon et al. 1987; Skogland 1983; Forchhammer et al. 2001). These delayed effects of cohort conditions on life-history traits might also be a consequence of delayed density dependence (Kruuk et al. 1999; Gaillard et al. 2003), which has been most commonly reported in north temperate ungulate populations (e.g. Pettorelli et al. 2001; Bonenfant et al. 2002), and empirical evidence for such effects is lacking in Mediterranean regions.

Supplemental feeding, the provisioning of high quality food to enhance individual and population characteristics (e.g. trophy size, number and survival of young, density), is a management practice that is used in many Iberian red deer (*Cervus elaphus hispanicus*) populations in south-central Spain (Gortazar et al. 2006; Vicente et al. 2007). The timing of supplementary feeding differs between regions throughout Europe: in northern areas, it is used to compensate for the negative effects of winter weather on the availability of natural foods (Schmidt and Hoi 2002; Putman and Staines 2004; in Mediterranean areas, it is used in summer (although food can be provided all year round). To the best of our knowledge, no study has evaluated short-term and cohort variations in fitness-related phenotypic traits by comparing food-supplemented and unsupplemented populations, which is crucial since resource availability mediates most of the density and weather effects on phenotypic traits (Pettorelli et al. 2006). In addition, supplementary feeding can reduce variation in survival and reproductive success among individuals and cohorts by reducing selection pressures (Schmidt and Hoi 2002).

In this study, we have evaluated the short- and long-term effects of rainfall and absolute population density on hinds in two of the southernmost populations of red deer in Europe. One of the populations received supplementary forage. We made four predictions: (P1) the body mass of hinds and the probability of gestation will be lower in the unsupplemented population than in that which is supplemented; (P2) the effects of season and local weather on deer life-history traits in Spain will differ from the patterns observed in populations at northern latitudes because the quantity and quality of the forage during winter is enhanced by the high accumulated precipitation that occurs in Mediterranean areas; (P3) the weather and absolute population density experienced by individuals early in their development will have long-term effects on their life-history traits; and (P4) supplemental feeding will act as a buffer against the effects of environmental stochasticity and density on the life-history traits of red deer hinds.

Materials and methods

Study areas and populations

The two study areas were located in Castilla-La Mancha, south-central Spain. The Mediterranean woodlands and scrublands in the area constitute a continuous distribution of largely independently managed private or public hunting estates, including natural preserves. The densities of deer populations are highly variable owing to game management practices, but densities are often above the natural carrying capacity (Acevedo et al. 2008). The study involved two red deer populations in fenced game estates 60 km apart. One estate (LM) was a private property devoted to game hunting (38°55′N, 0°36′E; 600–850 m a.s.l.) and the other (LQ) was a public hunting preserve to the north of the first (39°45′N, 4°15′E; 600–1,100 m a.s.l.). Table 1 summarizes the characteristics of the study areas and the red deer populations (source for habitat data: Corine Land Cover 2000, own data, see Acevedo et al. 2006). Both of the areas are hilly and the habitat of the estates is dominated by Mediterranean vegetation that is well adapted to high intra- and inter-annual variations in rainfall. Evergreen oak *Quercus ilex* are predominant and *Quercus pyrenaica* and *Quercus suber* are less common. In low-lying areas, there are scattered pastures and small plots of cropland. In Mediterranean habitats, pastures provide

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Table 1 Characteristics of two red deer (*Cervus elaphus hispanicus*) populations and the main habitat descriptors in two areas (LM and LQ) in south-central Spain

Descriptor	LM	LQ
Area (ha)	860	6,862
Supplementary forage	Yes	No
Faecal nitrogen (% ± SE) (2006)	2.22 ± 0.05	1.68 ± 0.08
Mean red deer absolute density (no. deer/100 ha ± SE, 1995–2008)	37.69 ± 1.51	31.58 ± 1.53
Mean red deer relative density (no. deer/ha Mediterranean *Quercus* spp. scrubland, 1995–2008)	37.69	31.58
Mean adult sex ratio (F:M)	1.07 ± 0.48	1.37 ± 0.25
Mean annual rainfall (mm, 1995–2008)	518.69 ± 53.91	593.55 ± 75.92
Dehesa and pastures (%)	38.27	15.01
Quercus spp. forest-scrub cover (%)	<1	38.16
Degraded scrub dominated by *Cistus* spp. (%)	50.17	12.12
Pine plantation (%)	11.55	35.39

good quality food during the period of vegetative growth of plants, mainly in winter and spring, depending on previous amounts of precipitation. In summer, pastures shrivel, nutritive quality decreases, and the Iberian red deer consequently becomes a specialized scrub forager (Bugalho and Milne 2003). Since 1989, the deer population on the 900-ha LM estate has received supplementary forage (protein-rich pellets) all year-round, whereas the deer population on the 6,860-ha LQ estate does not receive supplementary forage. At LM, supplementary forage has been provided by using elevated feeders ($n = 35$) distributed throughout the estate, which are easily accessed by red deer individuals from all age groups and sexes. Each day, game guards provided as many food pellets as the deer consume, and in summer, in addition to the pellets, alfalfa (*Medicago sativa*) hay is supplied on the ground. Some of the open areas (dehesas and pastures; Table 1) in the study areas are cultivated with graminaceous and leguminous plants. To quantify the quality of the diets on the estates, we measured faecal crude protein in September 2006, at the end of the summer period (7 faecal pools composed of 5 fresh faecal groups collected from the ground) on the food-supplemented estate, and 14 pools on the unsupplemented estate; Massey et al. 1994; Table 1).

The size of the deer population on the LM estate (Table 1) was estimated annually by using repeated direct counts at feeding sites at the end of July and during the rutting season (total = 8 days/year). The high-density population is strongly dependent on supplementary provisioning, especially at the end of summer when natural forage is limited. At that time, deer congregate around feeding sites and are counted at dusk. In the latitude of south-central Spain, the rutting season mainly occurs in September and October (the maximum peak in the frequency of conception occurs in late September and early October), and the birthing season is in late May and early June (authors, unpublished data). On the LQ estate, the size of the deer population was estimated annually in September by using distance sampling (Buckland et al. 2004; Distance 5.0 software). Red deer were counted by experienced observers (game guards) along nine transects twice in a year (mean length = 8.85 ± 1.11 SE km). The total area covered per year was 61.66 km and the sampling effort was 8.98 km/1,000 ha (Acevedo et al. 2006). The transects were distributed in a manner that was representative of the vegetation cover on the estate. The Hazard Rate Model with no expansion term was selected based on the AIC value (Buckland et al. 2004), goodness-of-fit tests (χ^2) and visual comparisons of histograms. The census data were manually grouped within an initial interval of 35 m followed by 20-m intervals, and truncated at 255 m to remove outliers and improve the fit of the model. Data were analysed as clusters. In our experience, both methods of estimating absolute density were the best choices for each estate (Acevedo et al. 2008). We expected absolute densities to be comparable between and within estates. In both the populations, adult sex ratios were slightly skewed toward females (Table 1).

Climatological data for LM were provided by the National Institute of Meteorology Station 317-E within the estate and the data for LQ were from the National Institute of Meteorology Station at Los Cortijos, 2 km south of the LQ estate. As inter-annual differences in weather may affect annual life-history traits, the data were therefore analysed based on the red deer reproductive phenology and the typical rainfall regimen in Mediterranean areas, from 1 September to 31 August of the following year, beginning with the wet season, when the rut occurs in Iberian red deer.

Sampling

In order to quantify the life-history traits of the deer populations, we used hinds that had been shot by gamekeepers to control density. Culling was non-selective, and biases in age or size were therefore unlikely (Martinez-Jauregui

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et al. 2005). A summary of sampling distribution across estates and years is shown in Fig. 1. All the females included in the analyses were ≥2 years old. A record was kept of the entire body mass (to the nearest kg) of each of the hinds shot during the hunting season (October–February). The reproductive state was assessed based on the presence of embryo, foetus, and corpora lutea) (Harder and Moorhead 1980). Age was estimated based on the histological examinations of incisors (Hamlin et al. 2000). For the statistical analyses, the data were assigned to biologically meaningful age classes (Landete-Castillejos et al. 2004): yearlings, subadults (3 years old), and adults (≥4 years old). The accuracy of age estimates based on incisors decreases with the age of the animal; therefore, the analyses were restricted to animals of ≤8 years old. This also allowed the confounding effect of ageing to be avoided.

Statistical analyses

A generalised linear model (GLM) as a function of estate, age-class, month, and their two-way interactions was used to assess between-estate (factor) differences in body mass (ln-transformed response variable). We fit the saturated model, which was modelled with a normal error and an identity link function. Detailed sample sizes are indicated in Fig. 1a (total $n = 1{,}597$).

Any short- or long-term relationships between population density and weather and deer body mass (ln-transformed response variable) were detected by carrying out generalised linear mixed models (GLMMs) using the data from each estate, separately, with the sampling year as the random variable (12 years with known absolute densities on both estates: 1995, 1997–1999, 2001–2008). Each year class included animals that were collected from October to February, e.g. "Year 1999" included hinds collected between October 1998 and February 1999. Age class was included as a categorical predictor. The dates of hunting varied from 1 October to 29 February and were measured as number of days since 1 October. In addition to the dates of the hunting season, we also included the square and the cubic terms in the analyses. Population densities at the time of collection and at the estimated time of birth were treated as continuous explanatory variables. To account for any delayed effects of rainfall, the models included annual precipitation in the year preceding the animals' estimated time of birth as a continuous explanatory variable (assuming that animals were born in year t_b, annual rainfall from June t_{b-1} to May t_b). We established multiple sets of a full array of models, each of which included one of the following probable sources of climatic variation as a continuous explanatory variable (assuming that animals were collected in year t): (1) rainfall in the previous autumn–winter (accumulated between September t and the following February), (2) rainfall in the previous spring (accumulated between March and May), and (3) rainfall in the summer (accumulated between June and September). These periods are biologically meaningful to red deer and plant phenologies in the Mediterranean region. Calving typically occurs in late May and early June, and

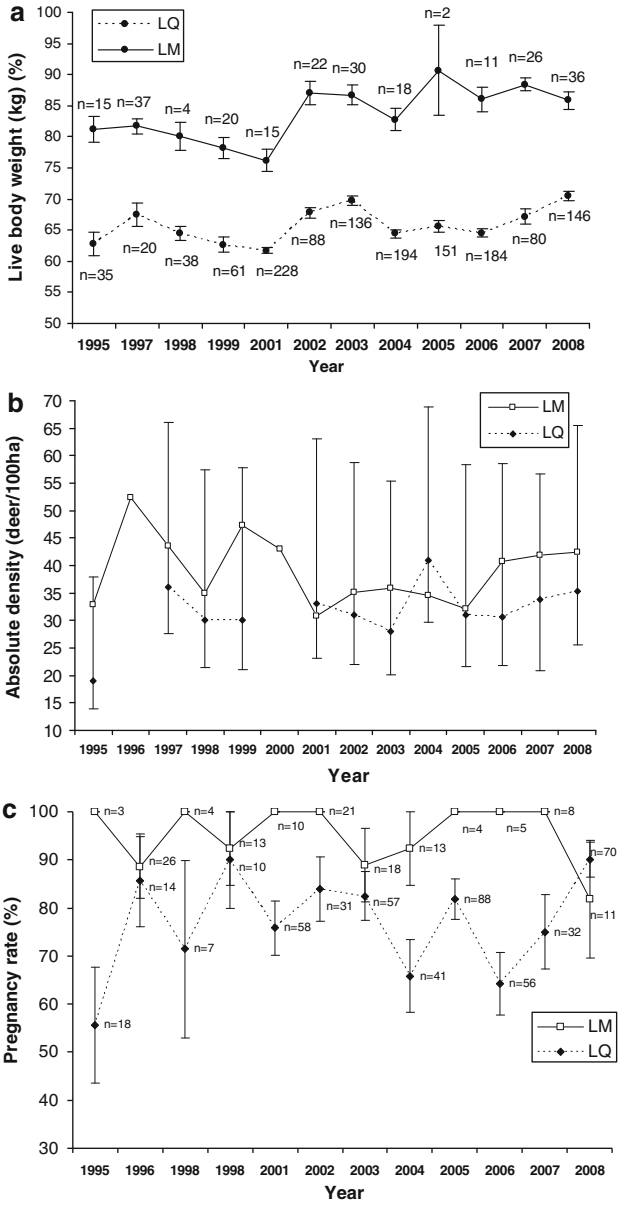

Fig. 1 Mean hind body mass (**a**), population density (**b**), and the prevalence of pregnancy (**c**), between 1995 and 2008 in two red deer (*Cervus elaphus hispanicus*) populations in south-central Spain. In 1996 and 2000, the density of the LQ population was not documented; therefore, these years were excluded from the statistical analyses. Annual sample size is indicated in (**a**) and (**c**). Body weights are the predicted values after the GLMM to partition the variance associated with female red deer body mass in relation to estate, month, and age-class in the two populations (Table 1)

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Table 2 Results from the GLMM to partition the variance associated with female red deer body mass in relation to estate, month, and age-class in two red deer populations in south-central Spain

Explanatory variable	*df*	*F*	*P*	Parameter estimates
Estate	1/1,585	188.85	<0.001	LQ = −0.22 ± 0.02
Days	1/1,585	5.42	0.02	−0.002 ± 0.001
Days^2	1/1,585	7.11	<0.01	0.001 ± 0.001
Days^3	1/1,585	4.53	0.03	−0.001 ± 0.001
Age-class	2/1,578	118.32	<0.001	Yearling = −0.19 ± 0.02, Subadult = −0.08 ± 0.02
Estate × days	1/1,583	0.05	0.82	LQ = 0.001 ± 0.001
Estate × age-class	2/1,580	26.29	<0.001	Yearling × LQ = −0.15 ± 0.02, Subadult LQ = −0.01 ± 0.02
Age class × days	2/1,578	0.71	0.49	Yearling = −0.01 ± 0.001, Subadult = −0.01 ± 0.001

The model was fitted using year ($Z = 2.12$, $P = 0.02$) as a random factor. Parameter estimates for the level of fixed factors were calculated using a reference value of 0 for adult level adult in the variable "age-class" and for LM (supplemented) in the variable "Estate". The overdispersion parameter was <1

df number degrees of freedom/density degrees of freedom

rutting occurs in September and October. The models included the terms weather × absolute density at birth and weather × absolute density at the time of collection in order to account for any interaction effects between population density and weather. Pregnancy may affect measurements of live body mass; the models therefore included the explanatory binary factor "pregnancy". All the females collected before December were assumed to be non-parous since the mass of foetus and uterus is to be assumed negligible at that time. We performed the full array of models, and best parsimonious models were selected based on Akaike's Information Criterion adjusted for small sample size (AICc, because the number of parameters was high in relation to sample size). Models that differed in AICc by two or less (ΔAICc ≤ 2) were assumed to have the same data support (Burnham and Anderson 1998). The sample sizes of hinds included in analyses from LQ and LM were 1,017 and 236, respectively. The residuals of the model were plotted against the explanatory variables in order to detect non-linear relationships.

We assumed that any effects of population density or rainfall on the likelihood of pregnancy would be mediated by body mass; we therefore evaluated the relationships between body mass (ln-transformed, explanatory variable), population density at birth (which was negatively correlated with body mass; see Table 3, below), rainfall near the time of birth (which was positively correlated with body mass; see Table 3, below), and reproductive state (dependent binary variable: 0 = not pregnant, 1 = pregnant). The model included days since 1 October as a continuous variable; estate (binary) and age-class as categorical predictors, and the two-way interactions among estate, rainfall, population density, and hind body mass; and the three-way interaction among estate, population density and rainfall. We fitted the saturated model, which was modelled with a binomial error and a logit link ($n = 1{,}192$). All the analyses were performed using SAS 9.0 statistical software, and the level for statistical significance was set at $P \leq 0.05$.

Results

Throughout the period encompassed by the study in south-central Spain (1995–2008), hind body mass (once adjusted for age, reproductive state, population density, and weather variables) was consistently higher in the food-supplemented LM population than in the LQ population (see models below) (Fig. 1a). Except in 2000 and 2004, population density at *t* (Fig. 1b) was higher in LM than in LQ, and in the LM population, the density was always >30 individuals per 100 ha. The prevalence of pregnancy at *t* was 90–100% in the LM, but was more variable in the LQ (Fig. 1c).

The between-estate comparative model revealed that between-estate differences in hind body mass were most pronounced in yearlings (Table 2; predicted body weight ± SD for yearlings, subadults and adults were 49.3 ± 2.4, 64.8 ± 3.5 and 71.4 ± 4.6 kg for the unsupplemented population, and 72.9 ± 3.2, 81.1 ± 3.3 and 90.6 ± 4.4 for the supplemented population, respectively). Hind body mass increased from October to February (Table 2; predicted body weights ± SD for October, November, December, January and February were 59.9 ± 9.1, 63.1 ± 8.5, 64.8 ± 8.3, 71.6 ± 7.9, 73.2 ± 7.9 kg for the unsupplemented population, and 81.8 ± 7.6, 81.7 ± 7.4, 79.9 ± 7.5, 84.0 ± 7.1, 89.0 ± 8.35 kg for the supplemented population, respectively).

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Effects of population density and rainfall on body mass

The most parsimonious model was ≤2 units smaller than the other models (not shown). In both populations, body mass increased with age (Fig. 2a). After controlling for reproductive state (positive effect of pregnancy) and age class (increased body weight with age class), body mass did not vary over time. Delayed effects of absolute density (the higher the density at birth, the lower the body mass at the time of collection) and rainfall (the higher the rainfall at birth, the higher the body mass at the time of collection) on hind body mass occurred in the unsupplemented population but not in the supplemented population (Table 3).

Effects of body mass, population density, and rainfall on pregnancy

The reproductive state model (Table 4), which included population density and weather at the time of birth (the outcomes from the body-mass models; Table 3), indicated that the probability of a hind being pregnant increased with body mass regardless of other factors such as age. As an indicative, most females >90 kg were pregnant. The probability of a hind being pregnant increased with age class and days from 1 October (percentage of pregnancies ± SE for October, November, December, January and February were 20.5 ± 2.7, 48.9 ± 2.4, 66.5 ± 2.7, 76.6 ± 3.4, 83.5 ± 2.6 kg for the unsupplemented population, and 31.8 ± 10.0, 90.9 ± 6.3, 100 ± 0.0, 87.0 ± 3.4, 95.3 ± 2.6 kg for the supplemented population, respectively). As the density increased at the time of birth, the probability of a hind being pregnant decreased in the unsupplemented population (Table 4), whereas such relationships were not evident in hinds in the food-supplemented population.

Discussion

In south-central Spain, the quantity, accessibility, and quality of forage markedly influences body growth and reproduction of red deer hinds, and is, thereby, likely to affect population dynamics. The responses of red deer life history traits to seasonal change and climatic variation differs from those found in populations in northern latitudes, which suggests that temporal variation in weather-related forage availability and population density on temperate-zone ungulates might differentially impose selection pressures and shape deer life-history traits across bio-geographical areas. The results of our study support the hypothesis that supplemental feeding acts as a buffer against the delayed effects of early life conditions.

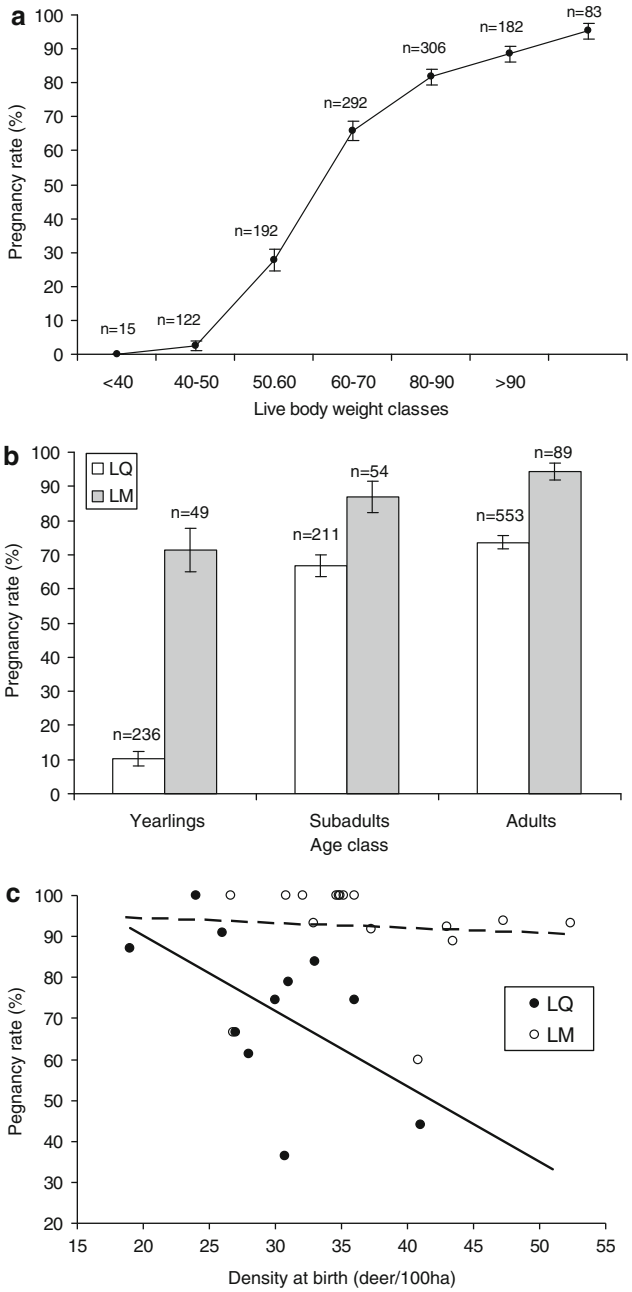

Fig. 2 The relationship between the prevalence of pregnancy (±SE) and **a** body mass (in 10-kg intervals), **b** age-class, and **c** population density at birth in hinds evaluated from December onwards, in two red deer populations in south-central Spain

Body mass growth and seasonal patterns

In south-central Spain, yearlings in the unsupplemented population were much lighter than the yearlings in the food-supplemented population, and the difference was somewhat less in the older age classes. The effect of estate was probably due to the influence of supplementary feeding, which accounted for most of the between-population

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Table 3 Results from GLMMs to partition the variance associated with body mass in supplemented and unsupplemented red deer populations in south-central Spain in relation to short- and long-term effects

Explanatory variable	*df*	*F*	*P*	Parameter estimates
LM estate (food-supplemented population)				
Age-class	2/226	62.28	<0.001	Yearling = −0.17 ± 0.02, Subadult = −0.09 ± 0.01
Reproductive state a.d.	1/229	54.64	<0.001	Not pregnant = −0.10 ± 0.01
LQ estate (unsupplemented population)				
Age-class	2/1,011	399.00	<0.001	Yearling = −0.32 ± 0.01, Subadult = −0.09 ± 0.01
Reproductive state a.d.	1/1,011	103.47	<0.001	Not pregnant = −0.1 ± 0.01
Density at birth	1/833	30.26	<0.001	−0.01 ± 0.001
Birth rainfall	1/898	13.24	<0.001	0.001 ± 0.001

Results are from the most parsimonious models based on AICc after performing the full array of models for each estate (population). The models were fitted with year (LM estate: $Z = 1.90$, $P = 0.03$, LQ estate: $Z = 2.07$, $P = 0.02$) as a random factor. Parameter estimates for the level of fixed factors were calculated based on a reference value of 0 for pregnant level in the variable "reproductive state". Overdispersion parameters were always <1. Reproductive state after December controlled for changes in body mass due to foetal-uterus development after December

df number degrees of freedom/density degrees of freedom, *a.d.* after December

Table 4 Results from the GLMM (full model) to partition the variance associated with the likelihood that a hind is pregnant in relation to estate, month, age-class, and body mass

Explanatory variable	*df*	*F*	*P*	Parameter estimates
Estate	1/1,142	0.87	0.35	−18.44 ± 10.87
Age-class	2/1,173	5.36	<0.01	Yearling = −0.70 ± 0.80, Subadult = −0.26 ± 0.78
Days	1/1,175	45.38	<0.001	0.03 ± 0.001
Body mass	1/1,174	25.08	<0.001	5.96 ± 2.36
Density at birth	1/769	1.32	0.25	−0.19 ± 0.11
Birth rainfall	1/994	1.68	0.19	−0.01 ± 0.01
Estate × density at birth	1/864	3.75	0.05	LQ = 0.23 ± 0.12
Estate × birth rainfall	1/979	2.22	0.13	LQ = 0.01 ± 0.001
Estate × days	1/1,175	1.43	0.23	LQ = −0.01 ± 0.01
Estate × age-class	2/1,176	1.86	0.15	LQ × Yearling = −0.71 ± 0.87, LQ × Subadult = 0.72 ± 0.81
Estate × body mass	1/1,174	0.04	0.84	LQ = 0.48 ± 2.47
Density at birth × birth rainfall	1/952	1.32	0.25	0.001 ± 0.001
Estate × density at birth × birth rainfall	1/1,021	2.21	0.13	LQ = −0.001 ± 0.001

The model was fitted with year ($Z = 1.6$, $P = 0.05$) as random factor. Parameter estimates for the level of fixed factors were calculated as indicated in Table 2. The overdispersion parameter was 1.04. The parameter estimates are at a logit scale. The tests of the main effects are not included since they are involved in the interactions

df number degrees of freedom/density degrees of freedom

differences observed in the life-history traits of red deer females.

Contrary to the pattern observed in northern deer populations where hinds lose body mass in autumn and winter because of adverse weather and reduced accessibility to food (e.g. Veiberg et al. 2004), the body mass of hinds in south-central Spain shows a marked increase between October and February. This trend in body mass may be influenced by seasonal changes in the availability of natural foods, which will vary depending on climate and plant phenologies (White 1978; Holmgren et al. 2001). In Mediterranean regions, the summer is the most challenging period for large herbivores because of limited precipitation and the relatively low quality food available (Bugalho and Milne 2003; Martinez-Jauregui et al. 2009). Thereafter, in autumn, *Quercus* spp. acorns become available, and pastures grow throughout the winter, which allow hinds to increase body mass between October and February.

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Body mass, population density and weather

In the unsupplemented red deer population in south-central Spain, local rainfall near the time of birth and hind body mass were positively correlated. The timing of the cohort effect (total rainfall in autumn, winter, and spring) coincided with the gestation period. In Mediterranean environments, high-quality pastures are scarce in summer and early autumn, and scrub vegetative growth ceases because of seasonal drought (Bugalho and Milne 2003). Precipitation (which irregularly occurs from autumn to spring) fosters the development of a profuse, high-quality herbage layer, activates vegetative growth in scrub vegetation and consequently dictates the availability of food throughout the year (Martinez-Jauregui et al. 2009), which can lead to a cohort effect through enhanced foetal development, calf weight at birth, and forage availability early in life. In the unsupplemented red deer populations in south-central Spain, hind body mass at the time of collection increased with the increasing amount of rainfall near the time of birth, but not with the rainfall at the time the animal was collected, as was observed in northern deer populations.

In unsupplemented ungulate populations, density at the time of birth may have a negative effect on hind body mass later in life (Post et al. 1997; Kruuk et al. 1999, for females; Bonenfant et al. 2002). Adverse environmental conditions caused by competition, or low maternal intrauterine or early life care during unfavourable conditions may generate differential density effects on cohorts (e.g. Mysterud et al. 2002; Gaillard et al. 2003). Thus, in south-central Spain, cohort effects in adult hind body mass were partially due to delayed density-dependence in the unsupplemented population. Long-term effects might persist throughout the life of hinds (no evidence of an age × density-at-birth interaction), and under unfavourable conditions individuals born in a 'bad' year cannot entirely compensate for their relatively poor start in life, possibly leading to a 1-year delay in reproduction. Complementary, long-term temporal changes in body mass in the unsupplemented population might have been influenced by persistent grazing and browsing by a large number of red deer, which affected the composition of the vegetation. Density-related cohort effects on adult body mass, either intra-uterine or during early life, are important because they are expected to affect population dynamics through their delayed effect on future reproduction and recruitment (Saether and Haagenrud 1983; Beckerman et al. 2002; Pettorelli et al. 2001).

Effects of body mass, population density, and rainfall on pregnancy

The prevalence of pregnancy was primarily an increasing function of body mass, after an adjustment for age (Table 4). The prevalence of pregnancy was consequently higher in the forage-supplemented population than in the unsupplemented population. In red deer, adult body mass is a strong predictor of fertility and reproductive success (Clutton-Brock and Albon 1989). Low body mass in autumn might reduce the likelihood of ovulation and successful gestation (Langvatn et al. 2004).

In the unsupplemented red deer population in south-central Spain, high population density at the time of birth had a negative effect on the prevalence of pregnancy. The conditions experienced by individuals in early life may thus have long-term effects on their life-history (delayed quality effect; sensu Gaillard et al. 2003), and differences in resource availability can lead to differences in reproductive tactics of populations. We have identified a link between population density early in life and an adult trait that is directly related to population dynamics (Gaillard et al. 2000a; Bonenfant et al. 2009). In male and female red deer, average lifetime reproductive success may differ among cohorts (Rose et al. 1998). When recruited into the population, individuals born in a good year can reproduce earlier (as yearlings), attain a higher body mass, and have higher reproductive success than individuals born in a poor year (Gaillard et al. 2000b). Compensatory growth is rare in ungulates (e.g. Toïgo et al. 2006), and hinds in the unsupplemented population that had low birth weights or had slow early growth rates might be compromised because of relatively low adult body mass, and would be likely to produce relatively fewer offspring in their lifetime, although long-term time-series studies are needed to clarify these issues (Gaillard et al. 2003). In the red deer populations in southern Spain, environmental conditions in the year of birth did not have a significant influence on the prevalence of pregnancy, which suggests that intra-specific competition for resources, rather than variation in abundance or "quality", led to a reproductive effect in the unsupplemented population. In contrast, in Norway, hind fecundity is correlated with winter weather when the females are in utero (Post and Stenseth 1999).

There is no precise data on density-dependent effects of food availability in red deer populations in Iberian Mediterranean areas, where high densities can affect plant communities (Trdan and Vidrih 2008) and increase the likelihood of disease (Gortázar et al. 2006). Deer densities in southern Spain (range = 5–70 animals per 100 ha; Acevedo et al. 2008) suggest that the densities in the populations that we studied (up to 40 and 50 deer per 100 ha in LQ and LM, respectively; Fig. 1b) might reflect an overabundance of deer (Côté et al. 2004). In the unsupplemented population, absolute densities >25 deer per 100 ha were associated with a considerable decrease in the prevalence of pregnancy.

We demonstrated that among-cohort differences in phenotypic quality translate into fitness differences only in the

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populations facing natural marked food limitations in Mediterranean habitats. Further research is needed to understand how early determinants of lifetime reproductive success differ between sexes (Kruuk et al. 1999) under different management situations, and how calf–age cohort morphometrics reflect animal density relative to carrying capacity or environmental events that influence carrying capacity (Strickland et al. 2008). Conservation and management plans for Iberian red deer should incorporate cohort effects and supplemental feeding practices, which might eliminate density- and climate-dependent effects and, subsequently, reduce natural selection pressures on red deer.

Acknowledgments We are very grateful to the gamekeepers and OAPN staff for their help with the fieldwork. This study was supported by grants from Junta de Comunidades de Castilla-La Mancha (JCCM) (project PAI07-0062-6611) and by the agreement between Yolanda Fierro and UCLM. Pablo Rodriguez-Hidalgo received financial support through an agreement between Fundación PRASA and Universidad de Córdoba. The research protocol complied with Spanish laws.

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